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Synergistic effects of warming and lower salinity on the asexual reproduction of reef-forming corals

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ABSTRACT

Tropical storms produce competent self-regenerating coral fragments capable of originating new coral colonies. These climatic events are predicted to increase in the future due to ocean warming, the main cause of coral bleaching. Estimated increases in precipitation will affect salinity at shallow reef areas which combined with ocean warming will aggravate the effects of coral bleaching. In this study the long-term effects of increased temperature (30 °C), low salinity (20 psu) and the combination of these stressors were investigated and compared to the control treatment (26 °C, 33 psu). Mortality, condition, growth, and regeneration ability of nine Indo-Pacific reef-forming coral species were assessed, for 60 days. The coral colonies used were kept in captivity for several years, providing information on their thermal and salinity history. Twenty replicate fragments were cut from each coral species' colony, weighed and glued to the top of a numbered expansion anchor and then acclimated to the experimental aquarium. Half of these fragments was inflicted with one circular injury in order to test its effects on mortality, condition, and growth rate and also to estimate tissue regeneration rates. The results showed that mortality rate was highest in the high temperature + low salinity treatment, reaching 100% for seven out of the nine coral species, in the first six days of experiment, 100% for *Psammocora contigua* on the 40th day and 75% for *Galaxea fascicularis* on the 60th day of experiment. Partial mortality was lowest for *P. contigua* and *G. fascicularis* in the low salinity treatment. These two coral species also presented the best coral condition. Coral fragments growth rates decreased as temperature increased and salinity decreased except for *G. fascicularis* fragments that showed similar growth rates at 26 °C and 30 °C for both salinities. Regeneration rates increased with temperature being highest in the high temperature treatment and lowest at 20 psu. It was concluded that *G. fascicularis* and *P. contigua* are the most resilient to low salinity. *G. fascicularis* fragments were the only ones that withstood the synergistic effects of high temperature and low salinity and are likely to become dominant through asexual reproduction in the Indo-Pacific coral reefs in a warmer ocean, especially in coastal areas prone to low salinity episodes.

1. Introduction

Coral reefs are one of the largest and most diverse reservoirs of biodiversity throughout the world (Baker et al., 2008; Prada et al., 2010). Scleractinian corals are the dominant taxonomic group of tropical coral reef ecosystems, as their association with symbiotic intracellular dinoflagellate (zooxanthellae, *Symbiodinium* spp.) (Hoegh-Guldberg, 2011) is responsible for the high productivity and structural complexity of coral reefs (Bruno and Bertness, 2001; Idjadi and Edmunds, 2006).

Coral reefs worldwide are among the most vulnerable ecosystems to global climate change (Hoegh-Guldberg et al., 2007; Hughes et al., 2003; West and Salm, 2003). Climate change is leading to rising sea surface temperatures, low seawater salinities, and ocean acidification (Faxneld et al., 2010; Hoegh-Guldberg et al., 2007; Hughes et al., 2003; IPCC, 2014) compromising scleractinian corals' growth and mortality (Carpenter et al., 2008; Padilla-Gamiño et al., 2013). Currently, one-third of reef-building corals experience high extinction risk from climate change (Carpenter et al., 2008).

Coral bleaching episodes are strongly associated with sustained and anomalously high sea surface temperatures (Hoegh-Guldberg, 1999; Jokiel and Coles, 1974; Loya et al., 2001; McClanahan et al., 2009). Bleaching episodes can also be triggered by a range of other environmental stress factors, including salinity (Wild et al., 2011). Localized coral bleaching events due to low seawater salinities at shallow reef areas (Kerswell and Jones, 2003), following intensive rainfall during

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tropical storms, have been reported throughout the world (Blakeway, 2004; Coles and Jokiel, 1992; Goreau, 1964; Jokiel et al., 1993; van Woesik et al., 1995). These events' effects may be exacerbated during episodes of elevated seawater surface temperatures (Faxneld et al., 2010; Xiubao et al., 2009).

Coral bleaching is a stress reaction that describes the morphological changes that occur during the breakdown of the coral-zooxanthellae association (Glynn, 1991; Desalvo et al., 2008). Upon bleaching, corals lose a considerable number of their zooxanthellae and/or photosynthetic pigments per algal cell (Glynn, 1993; Hoegh-Guldberg, 1999), giving the colony a white appearance (Brown, 1997). As healthy corals normally supplement their metabolism through the provision of photosynthetic compounds by zooxanthellae (Davy et al., 2012), bleaching culminates in significant reductions in zooxanthellae photosynthesis accompanied by drastic changes in physiology (Lesser and Shick, 1989; Muscatine et al., 1991). Therefore, bleached corals usually decrease skeletal calcification rate (Leder et al., 1991), tissue regeneration ability (Meesters and Bak, 1993), growth rates and reproductive capacities (Baird and Marshall, 2002; Szmant and Gassman, 1990), as well as increased susceptibility to disease (Harvell et al., 1999). If a heat stress event is prolonged or particularly severe it may result in partial or complete coral mortality (Brown et al., 2002; Hoegh-Guldberg, 2011; Jones, 2008; Wooldridge, 2014). On the other hand, when corals survive the heat stress event and the stress has ended, the symbiotic association can be re-established and their physiology may be restored (Grottoli et al., 2014; Schoepf et al., 2015). Mass coral bleaching episodes are responsible for live coral cover depletion in many parts of the world (Aronson et al., 2002; Baker et al., 2008; Bruno and Selig, 2007; Burt et al., 2011), resulting in reef community structure shifts that reduce biodiversity in the marine tropics (Baker et al., 2008; Eakin et al., 2009; Norström et al., 2009; Schutte et al., 2010).

Average sea temperatures surrounding coral reefs are projected to increase by 1–3.7 °C by the end of the century (IPCC, 2014, 2018), as are the frequency and severity of thermally induced coral bleaching events in most tropical oceans (Crabbe, 2008; IPCC, 2014, 2018). Globally, thermally induced bleaching is projected to occur annually in most oceans within 20–40 years (Crabbe, 2008; Császár et al., 2010). Warmer seas are likely to drive more intense and frequent tropical storms (hurricanes, cyclones, typhoons) (Emanuel, 2005; Hughes et al., 2003; Walsh and Ryan, 2000) with larger peak wind speeds and heavier precipitation (Emanuel, 2005; IPCC, 2014). The frequency and maximum intensity of categories 4 and 5 storms are also expected to increase (0–25%) besides an increase in tropical cyclones rainfall rates (5–20%) (Christensen et al., 2013; IPCC, 2014), which may lead to drastic changes in inshore salinity levels (Haapkylä et al., 2011; Milly et al., 2002).

Coral community maintenance, repopulation, and recovery are greatly dependent on both sexual and asexual reproductive processes (Glynn et al., 2017). While sexually produced larvae may establish highly dispersed and genetically diverse populations, asexual recruitment through fragmentation or fission may allow rapid expansion of a population locally and enable the propagation of well-adapted genotypes within an area (Baums et al., 2006; Miller and Ayre, 2004), or assist in the colonization of habitats unfavorable for larval settlement (Heyward and Collins, 1985). The ratio of sexual and asexual recruitment is expected to change over the geographic range of a species, depending on the frequency of sexual recruitment, genet longevity (Coffroth and Lasker, 1998), and disturbance effects (e.g. ENSO events, global warming, tropical storms; Baums et al., 2006). Under current changes in climatic conditions and unparalleled anthropogenic disturbance to reef ecosystems, the success of sexual reproduction may be low (Hoegh-Guldberg, 2004; Albright and Mason, 2013; Levitan et al., 2014). This way, a rapidly changing environment may favor alternative asexual mechanisms of propagation.

Tropical storms are favorable to the propagation and expansion of branching coral forms by asexual reproduction of storm-generated fragments across the reef (Highsmith, 1982; Highsmith et al., 1980; Lirman, 2000; Tunnicliffe, 1981), which later re-attach to the substrate, growth and form a new colony (Foster et al., 2007). Asexual reproduction by fragmentation of plate and massive coral forms has also been noticed (Foster et al., 2007, 2013; Highsmith, 1980). Over the long term, fragmentation can decrease the risk of genotype mortality through the spatial separation of the fragments (Harper, 1977; Hughes, 1983). Given the current predictions of more frequent and intense storms it is reasonable to assume that coral asexual reproduction will increase through coral fragmentation.

Rapid coral fragments' recovery is attained when asexual reproduction and regeneration are possible (Highsmith, 1982). Following disturbance, the production of new colonies by fragmentation of existing colonies is considered to be a primary mode of reproduction and local distribution among major reef-building corals (Bruno, 1998; Connell and Keough, 1985; Highsmith, 1982; Pearson, 1981; Tunnicliffe, 1981). Asexual regeneration after fragmentation prevails in reef communities as it is observed in many coral species (Fong and Glynn, 2000; Glynn and Fong, 2006; Tunnicliffe, 1981). Fragmentation may also be adaptive, since it has been incorporated into the life history of a considerable number of the most successful scleractinian corals (Highsmith, 1982).

There is a noticeable variation in the extent of bleaching, both within and between coral colonies on a reef (Hoegh-Guldberg and Salvat, 1995; Marshall and Baird, 2000). Interspecific variability in reef-building corals susceptibility to heat stress can depend on the zooxanthellae clades (Rowan et al., 1997), colony morphology (Dias et al., 2018; Lang et al., 1992), tissue thickness (Hoegh-Guldberg, 1999; Loya et al., 2001), colony size (Edmunds, 2005; Shenkar et al., 2005), metabolic rates (Gates and Edmunds, 1999), mucus production rates (Fitt et al., 2009; Wooldridge, 2009), tissue concentration of fluorescent pigments (Salih et al., 1998), seasonality (Scheufen et al., 2017), heterotrophic feeding capacity (Grottoli et al., 2006; Levas et al., 2013), and coral species (Dias et al., 2018; Marshall and Baird, 2000). In addition, different tolerance of scleractinian corals to low salinity depends on coral species (Berkelmans et al., 2012; Faxneld et al., 2010; Lirman and Manzello, 2009; Moberg et al., 1997), colony morphology (True, 2012; van Woesik et al., 1995), and their polyp retraction response under osmotic stress (Muthiga and Szmant, 1987). Nevertheless, not all the different descriptors proposed to explain the different susceptibility of scleractinian corals to both heat and hyposaline stressors are truly sustained by experimental evidence.

This differential tolerance of scleractinian corals to the effects of heat and hyposaline stressors may lead to dramatic changes in the community structure of coral reefs (Loya et al., 2001; True, 2012), however, few studies have been conducted on the combined effects of temperature and salinity on scleractinian corals (Coles and Jokiel, 1978; Faxneld et al., 2010; Hoegh-Guldberg and Smith, 1989; Porter et al., 1999; Xiubao et al., 2009), and only Xiubao et al. (2009) estimates their long-term effects (10 days). In addition, these studies only include one to two coral species with no contrasting morphologies.

In order to evaluate the effects of global (i.e. temperature) and localized (i.e. salinity) stressors altered by global climate change on reef coral communities, we submitted nine reef-building corals to high temperature (30 °C), low salinity (20 psu), and their combination compared to control treatment (26 °C, 33 psu) for 60 days and assessed how these environmental parameters affected their mortality, condition, growth, and regeneration ability. To our knowledge, this is the first study to assess the long-term effects of high temperature and low salinity on the mortality, coral condition, growth and regeneration post-fragmentation in nine common and widely distributed reef-building corals of the Indo-Pacific oceans (Veron, 1990, 2000). We hypothesize that (i) mortality, condition, growth, and regeneration rates of the coral fragments vary as a function of species, temperature, salinity, and injury (ii) high temperature and low salinity have a synergistic negative effect on corals' mortality, condition, growth, and regeneration rates.

Such an assessment is critical to understand the differential vulnerability of reef-forming coral species to these two different stressors and can help reveal future coral species dominance and decline and determine future biodiversity shifts on coral reef ecosystems.

2. Material and methods

2.1. Coral specimens and maintenance conditions

This study investigated nine common and widely distributed Indo-Pacific coral species (Veron, 1990, 2000) with different morphologies: three plating species (*Montipora capricornis* brown morphotype (BM), *Turbinaria reniformis,* and *Echinopora lamellosa*), one massive species (*Galaxea fascicularis*), four branching species (*Acropora tenuis, Pocillopora damicornis, Stylophora pistillata,* and *Psammocora contigua)*, and one encrusting species (*Montipora capricornis* green morphotype (GM)). These coral species were chosen in order to use the largest number of species available at Oceanário de Lisboa with different colony morphology, a characteristic mentioned as having influence in coral species susceptibility to heat and hyposaline stress (Loya et al., 2001; True, 2012). Coral species identification was made according to Veron (2000). Information relative to the coral species in study and their zooxanthellae was taken from the literature and given in Tables 1 and 2. The coral colonies used in the present study have been kept in captivity in a coral stock aquarium at Oceanário de Lisboa (Portugal) for several years, which gave us information on their thermal and salinity history. Also, as all the coral colonies were subjected to the same homogeneous conditions during growth, we could investigate the species-specific differences to the experimental treatments.

The coral stock aquarium system includes two connecting tanks (3500 L) where the coral collection is kept and is fitted with a degasification tower and Fiji live rock (0.5 m^3) for biological filtration. For water circulation purposes, a Hayward 1hp water circulation pump provided a turnover rate of 3.5 times per hour to the two identical tanks that hold the coral collection. An AquaMedic Turbo 5000 protein skimmer helps keeping nutrient concentrations low and increased surface water motion in the aquarium is accomplished by using two 250 L Carlson surge devices. This aquarium is also fitted with a calcium reactor (25–35 L/h). Lighting requirements are attained by using four Litpa Jet5 floodlight with an AquaMedic 400 W HQi lamp (10000 K) fitted on each on a 12 h light/12 h dark cycle. Eight air-stones are used in the aquarium to ensure good oxygen concentrations.

Photosynthetically Active Radiation (PAR) levels were measured with a spheric quantic sensor (LI-193SA) and a data logger (1400 model) and varied between 300 and 350 $\mu E.m^{-2}s^{-1}$ in the 400–700 nm waveband. Water quality parameters such as water temperature, pH and salinity are measured on a daily basis. Water samples are also weekly analyzed to determine ammonium, nitrites, nitrates, calcium concentration as well as oxygen concentration and saturation and alkalinity. The average values for the water quality parameters of the coral stock system are the following: water temperature at 25.0 °C, pH at 8.16, salinity at 33.0 psu, alkalinity at 100 mg l^{-1}, ammonia at 0.00 mg l^{-1}, nitrites at 0.003 mg l^{-1}, nitrates at 0.150 mg l^{-1}, calcium concentration at 346 mg l^{-1}, oxygen saturation at 105% and oxygen concentration at 7.1 mg l^{-1}. Calcium concentration levels are kept through daily 15 L *kalkwasser* additions alongside the effluent water of the running calcium reactor aforementioned. Salinity is measured using a WTW Inolab conductivity meter Level 1 and is maintained with weekly additions of a saturated saline solution. Whenever alkalinity levels are below 100 mg l^{-1} sodium bicarbonate is added to the system. Aquarium cleaning routines are performed every week and a half and include a 15% water change, egg-crate replacement, bottom sand siphoning and cleaning of the tank walls.

Table 1
Characteristics of the coral species in study. Data taken from LaJeunesse et al. (2004), Loya et al. (2001), Richmond (1997), Veron (1990, 2000).

Coral species	Family	Colony morphology	Tissue thickness	Skeleton morphology	Reproductive mode	*Symbiodinium* clade	Depth range	Habitat
A. tenuis	Acroporidae	branching	thin	Axial corallites are long and tubular; radial corallites are arranged in a neat rosette and have slightly flaring lips (0.8–1.2 mm diameter)	spawner	C, D	8–20m	Upper reef slopes, shallow subtidal habitats
M. capricornis (BM)	Acroporidae	plating	thin	Corallites are immersed (0.6–1.0 mm diameter)	spawner	C	2–20 m	Lagoons, shallow tropical reef environments
M. capricornis (GM)	Acroporidae	encrusting	thin	Corallites are immersed (0.6–1.0 mm diameter)	spawner	C	2–20 m	Lagoons, shallow tropical reef environments
T. reniformis	Dendrophylliidae	plating	thin	Corallites are widely spaced, thick walled, Immersed to conical in shape (2.8–4.2 mm diameter)	spawner	C, D	2–15 m	Fringing reefs where the water is turbid
E. lamellosa	Merulinidae	plating	thin	Corallites are relatively thin walled and small (2.3–3.4 mm diameter)	spawner	C, D	1–40 m	Shallow water habitats with flat substrates
G. fascicularis	Euphylliidae	massive	thick	Corallites are of mixed sizes, usually with 5.8–10.7 mm diameter with numerous septa reaching the corallite centre	spawner	C, D	1–15 m	Reef environments protected from strong wave action
P. damicornis	Pocilloporidae	branching	thin	Corallites are immersed (0.8–1.0 mm diameter)	brooder	A, B, C, D	1–20 m	Shallow waters (exposed reef fronts, mangrove swamps)
S. pistillata	Pocilloporidae	branching	thin	Corallites are immersed, conical or hooded (0.9–1.4 mm diameter)	brooder	A, C, D	1–15 m	Shallow water reef environments exposed to strong wave action
P. contigua	Psammocoridae	branching	thin	Corallite structures are fine and corallites are shallow (1.1–1.5 mm diameter)	spawner	C, D	0–30 m	Shallow reef environments and soft substrate

Table 2
Published data of zooxanthellae density and chlorophyll *a* concentration for the coral species in study. No data were found for *Montipora capricornis* (both morphotypes).

Coral species	Zooxanthellae density ($\times 10^6$ cells cm^{-2})	Chorophyll *a* $area^{-1}$ (μg cm^{-2})	Cholophyll *a* $cell^{-1}$ (pg $cell^{-1}$)	Reference
Acropora tenuis	–	0.33–0.82	–	Abrego (2008)
	0.28–0.39	2.20–6.90	–	Tanaka et al. (2014)
	–	6.98–13.97	–	Vogel (2015)
Turbinaria reniformis	0.37–0.87	–	–	Béraud et al. (2013)
	0.47–0.76	–	–	Courtial et al. (2017)
	0.76–1.37	–	–	Ferrier-Pagès et al. (2010)
	0.59	3.30	–	Grottoli et al. (2018)
	0.28–0.50	–	6.61–11.63	Hoadley et al. (2016)
	0.61–0.80	3.50–4.75	–	Schoepf et al., 2013
	3.51–5.27	0.93–2.09	–	Tolosa et al. (2011)
	–	1.21	–	Treignier et al. (2008)
	0.91–1.60	–	–	Tremblay et al. (2015)
	0.31–0.59	–	–	Ulstrup et al. (2006)
	0.54–0.62	3.40–5.24	–	Zawada (2015)
Echinopora lamellosa	2.22	–	–	Li et al. (2008)
	0.06–0.17	–	–	Titlyanov et al. (2001)
Galaxea fascicularis	–	–	8.81–9.00	Al-Moghrabi et al. (1995)
	1.24–3.18	–	–	Borell et al. (2008)
	12.00	–	–	Brown et al. (1995)
	1.80–2.91	–	–	Ferrier-Pagès et al. (2010)
	0.58–1.00	2.33–4.16	4.24–4.56	Hidaka and Miyagi (1999)
	0.48–1.12	–	–	Higuchi et al. (2008)
	2.90	–	6.75	Hii et al. (2009)
	2.65–6.45	–	–	Mwaura et al. (2009)
	–	1.00–4.10	–	Schutter et al. (2010)
	2.58–3.17	3.66–4.21	1.54–1.81	Schutter et al. (2011)
	2.60	–	–	Stimson et al. (2002)
	0.10–1.02	–	–	Xiubao et al. (2009)
Pocillopora damicornis	1.85–2.32	–	–	Courtial et al. (2017)
	2.00	–	0.50	Glynn and D'Croz (1990)
	1.70	–	–	Glynn et al. (1992)
	0.80–8.30	2.04–12.96	1.81–2.90	Hueerkamp et al. (2001)
	0.31–0.51	3.00–9.00	–	Jokiel et al. (1982)
	0.42–1.12	–	2.79–3.30	Jones et al. (2000)
	0.53–0.79	7.44–13.00	13.21–19.92	Kinzie et al. (1984)
	1.86	–	–	Li et al. (2008)
	0.57–1.87	0.87–3.92	1.21–4.23	Mayfield et al. (2013)
	0.35–2.33	–	–	Mwaura et al. (2009)
	–	0.26	–	Nakano et al. (2009)
	0.29	2.75–3.17	–	Schoepf et al. (2013)
	0.53	–	–	Schrameyer et al. (2014)
	0.40	–	–	Stimson and Kinzie (1991)
	1.10	–	–	Stimson et al. (2002)
	1.20	–	–	Stimson (1997)
	0.73–1.10	–	–	Titlyanov and Titlyanova (2002)
	1.66	–	–	Titlyanov et al. (1996)
	0.32–1.01	–	–	Ulstrup et al. (2006)
Stylophora pistillata	0.83–1.02	–	–	Amir and Mohamed (2017)
	0.55–0.67	–	–	Ammar et al. (2013)
	1.03–1.94	–	–	Borell et al. (2008)
	–	3.60	–	Dubinsky et al. (1984)
	0.06	1.82	3.00	Dubinsky et al. (1990)
	1.60	3.60	2.20	Falkowski and Dubinsky (1981)
	1.40–1.89	–	–	Ferrier-Pagès et al. (2010)
	0.83–1.02	–	–	Fitt et al. (2009)
	3.02–3.38	–	–	Godinot et al. (2011)
	0.47–0.52	–	7.23–7.61	Hoegh-Guldberg and Smith (1989)
	0.22–0.74	–	–	Jimenez et al. (2012)
	1.24–1.34	–	–	Jones et al. (1999)
	0.18–1.01	0.70–2.46	0.88–1.60	Kerswell and Jones (2003)
	0.50	–	–	Kuroki and van Woesik (1999)
	1.11	2.61	2.43	Muscatine et al. (1989)
	1.04	3.11	2.98	Porter et al. (1984)
	1.10	–	–	Stimson et al. (2002)
	0.69–1.60	–	–	Titlyanov and Titlyanova (2002)
	0.68	–	–	Titlyanov et al. (1996)
	1.42–1.97	–	–	Tremblay et al. (2012)
	2.73–5.38	–	–	Tremblay et al. (2015)
Psammocora contigua	1.09	–	–	Li et al. (2008)
	1.90	–	–	Stimson et al. (2002)

2.2. Experimental setup

The experiments were conducted at Oceanário de Lisboa, Portugal (www.oceanario.pt).

To test the effects of species on mortality, condition, growth, and regeneration rates, 20 replicate fragments were cut from each coral colony, using a pincer or a pair of pliers. For the plate, massive, and encrusting coral colonies the fragments were obtained by cutting approximately 30 mm sided squares and the fragments for the branching corals were cut approximately 20–40 mm in length. These procedures were performed in order to represent the fragmentation of the coral species colonies during a tropical storm event. Afterwards, the coral fragments were placed over egg crate panels in the coral stock aquarium until acclimation to the experimental aquarium.

The live wet mass of each coral fragment was obtained by blotting it with a paper towel to remove excess seawater, then weighing it in air on an electronic balance to the nearest 0.01 g (Titlyanov et al., 2005). Each coral fragment was glued with epoxy putty to the top of a numbered and pre-weighed nylon expansion anchor. Placement of the coral fragment differed with morphology: plate, massive, and encrusting fragments were placed in horizontal position and the branching fragments in vertical position. These procedures were performed in order to reduce to the lowest possible the dead tissue area resulting by epoxy putty application according with the coral morphology. Then, the set (anchor + coral fragment) was weighed to remove the epoxy putty weight off the calculations and placed back over egg crate panels in the coral stock aquarium to recover from the handling procedures for one day before acclimation to the experimental aquarium.

To determine the long-term response of the nine coral species to the individual and combined effects of high temperature and low salinity the coral fragments were exposed to different treatments: (a) control (26 °C, 33 psu) (26.1 ± 0.2 SD; 33.0 ± 0.1 SD), (b) high temperature (30 °C) (30.2 ± 0.5 SD), (c) low salinity (20 psu) (20.0 ± 0.1 SD), and (d) high temperature + low salinity (30 °C, 20 psu) (29.9 ± 0.2 SD; 20.0 ± 0.1 SD). Twenty coral fragments of each coral species were exposed to each of the different treatments for 60 days. Coral fragments were acclimated one hour per °C above the temperature of the coral stock aquarium (25 °C). Coral reef-flat communities can experience temperature changes of 1 °C hour^{-1} during spring tides (Berkelmans and Willis, 1999), and most of the coral species in this study colonize the reef-flat zone (Brown and Suharsono, 1990), so we used this heating rate to be similar to the conditions that most of these corals would experience in their natural environment. In order to standardize, this heating rate was applied for all the coral species. Also, studies have shown that salinity can drop very quickly in nearshore areas after heavy rainfalls (from 30 to 15 psu within 24 h; Jokiel et al., 1993), especially when concurrent with low tides (min to hours; Kerswell and Jones, 2003). Thus, we allowed the coral species to acclimate from 33 psu to 20 psu during five hours in both low salinity and high temperature + low salinity treatments. The coral fragments were placed 2 cm apart from one another and organized by coral species to avoid contact between fragments of the same and/or different coral species.

The experimental aquarium (400 L) was fitted with a sump (280 L) filled with bioballs for biological filtration in which a Hailea 500 chiller and two Fluval M300 heaters controlled water temperature. For water circulation purposes, an AquaMedic OceanRunner 3500 pump provided a turnover rate of 5 times per hour. An AquaMedic Turboflotor 5000 Shorty protein skimmer helped keeping nutrient concentrations low and increased surface water motion in the aquarium was accomplished by using an AquaClear 110 powerhead. Lighting requirements similar to the coral stock aquarium were attained by using a Litpa Jet5 floodlight with an AquaMedic 400 W HQi lamp (13000 K) on a 12 h light/12 h dark cycle. An air-stone was used in the aquarium to ensure good oxygen concentrations.

Photosynthetically Active Radiation (PAR) levels were measured with a spheric quantic sensor (LI-193SA) and a data logger (1400 model) and varied between 320 and 345 μE.m^{-2}s^{-1} in the 400–700 nm waveband. The experiments were conducted under low light conditions (320–345 μE.m^{-2}s^{-1}) in order to minimize synergistic effects with high light conditions (Fitt et al., 2001; Scheufen et al., 2017). Water quality parameters such as water temperature, pH and salinity were measured on a daily basis. Water samples were also weekly analyzed to determine ammonium, nitrites, nitrates, calcium concentration as well as oxygen concentration and saturation and alkalinity. These parameters were maintained as follow: pH at 8.3, alkalinity approximately at 100 mg l^{-1}, nitrites between 0.002 and 0.003 mg l^{-1}, nitrates between 0 and 1 mg l^{-1}, calcium concentration between 389 and 401 mg l^{-1}, oxygen saturation between 101 and 104% and oxygen concentration between 6.6 and 7.1 mg l^{-1}. Salinity was measured using a WTW Inolab conductivity meter Level 1 and it was maintained with daily balanced additions of reverse osmosis freshwater and filtered artificial seawater. Whenever alkalinity levels were below 100 mg l^{-1} sodium bicarbonate was added to the system. Aquarium cleaning routines included expansion anchors cleaning with a toothbrush and egg crate replacement, at least 3 times a week.

To test the effects of injury on mortality, condition, and growth rate of the nine coral species, ten coral fragments of each species were used as controls (undamaged) and the other ten fragments were inflicted with circular injuries designed to simulate damage by predators, after being acclimated to the experimental aquarium. These artificial injuries were 3 mm in diameter and were performed using a Dremel rotatory tool with a cutting disk. Only one injury was inflicted in the middle section of each coral fragment to avoid edge effects. After these procedures, all fragments were placed over two 40 × 40 cm egg crate panels suspended 15 cm below the water surface of the experimental aquarium.

2.3. Analytical procedures

2.3.1. Mortality and coral condition assessments

Mortality was quantified as the percentage of dead fragments and partial mortality was visually quantified by estimating the percentage of dead area in the coral fragments and establishing four classes: [0,25%], [25,50%], [50,75%], and [75,100%]. The coral condition of each coral species was visually assessed according to four categories: normal, pale, bleached and dead (Jokiel and Coles, 1974). Normal corals were defined as having their normal coloration while pale corals showed a visible decrease in pigmentation. Bleached corals were considered as totally colorless and dead corals had no tissue at all. Mortality was assessed every day of the experiment with only the relevant days indicated in the results, whereas partial mortality and coral condition were assessed every 20 days until the end of the experiment. Mortality, partial mortality, and coral condition were assessed always by the same person to remove observer bias.

2.3.2. Growth rate measurements

The coral fragments were weighted both in the first and last day of experiment in order to calculate the growth rate for each coral fragment. The relative growth rate (RGR), expressed as daily biomass increase, was calculated using the formula:

$$RGR = [\ln(Wf/Wi)]/[(tf - ti)] \times 100$$

where Wi is the initial weight, Wf is the final weight and tf and ti is the time interval between the starting and end date (Marinho-Soriano et al., 2006).

2.3.3. Regeneration rate of injuries

The size of the coral fragments' injury was measured immediately upon their infliction and every 20 days afterwards until the end of the experiment. Injury recovery was quantified through photograph analysis and the injury area was estimated using ImageJ image software. Whenever the injury was not visible, due to partial mortality or

bleaching, that species fragment would not be considered for regeneration purposes. The tissue regeneration rates (Ts) were estimated after complete fragment regeneration or the last point in time each fragment was still alive. These regeneration rates were obtained by calculating the difference between the areas of the recovered surfaces (Ra) for any given interval (T_1 and T_0 in days), as follows (Cróquer et al., 2002):

$$Ts = [Ra(T_1) - Ra(T_0)]/(T_1 - T_0)$$

2.4. Statistical analyses

A four-factor nested PERMANOVA (Anderson, 2001) was used, with Euclidean distance to calculate the similarity matrix (coral species, temperature, salinity and injury were fixed factors with temperature, salinity and injury nested in coral species) that was used to test whether coral fragments' partial mortality, growth and regeneration rates were affected by coral species, temperature, salinity, and injury (for partial mortality and growth rate) and was run for 9999 permutations. Analyses were performed using PERMANOVA + for PRIMER v6 (PRIMER-E Ltd., Plymouth). Post-hoc pair-wise comparisons were then performed using PERMANOVA to compare between treatments and coral species. Differences were considered significant at $p < 0.05$.

3. Results

The factor injury had no effect on the partial mortality and growth rate of the coral fragments (PERMANOVA $p > 0.05$, Table 3) and therefore it was not considered as a factor in further analysis, with no separation between control and injured fragments.

3.1. Mortality and coral condition

3.1.1. Mortality

The coral species *A. tenuis* was the only one showing mortality at the control treatment (10%, Table 4). The fragments of *P. damicornis* and *S. pistillata* presented 100% mortality by the 60th day in the high temperature treatment (Table 4). In the low salinity treatment most of the coral species perished, with the exceptions of *G. fascicularis* and *P. contigua* (30% and 5%, respectively; Table 4). In the high temperature + low salinity treatment, *G. fascicularis* was the only survivor (survival rate of 25%, Table 4). In the single stressor treatments, mortality was higher in the low salinity treatment and lower in the high temperature treatment, which indicates that, in comparison with the control treatment, the decrease in salinity (−13 psu) was more detrimental to the coral species than the increase in temperature (+4 °C). In the multiple stressors treatment, high temperature + low salinity, not only the corals species presented higher mortality percentage but also they presented it earlier in this treatment than in the single stress treatments (Table 4), which indicates that these two environmental variables acted synergistically.

3.1.2. Partial mortality

Partial mortality was significantly affected by the independent effects of coral species, temperature, and salinity (PERMANOVA $p < 0.05$, Table 3). There was also a significant effect of the interactions of temperature and salinity (PERMANOVA $p < 0.05$, Table 3).

There were significant differences in partial mortality between temperatures for most of the coral species (PERMANOVA $p < 0.05$, Table 3), exception of *A. tenuis* and *T. reniformis* fragments (PERMANOVA pair-wise $p > 0.05$, Table 5). At 30 °C, partial mortality was in general higher than at 26 °C, with the exception of *E. lamellosa* (Table 5), which indicates that the increase in temperature of 4 °C was detrimental for most of the coral species in study.

Since the 20th day of experiment there were significant differences in partial mortality between salinities for all species (PERMANOVA $p < 0.05$, Table 3). At 20 psu, most coral species presented partial mortality near 100% on the 20th day, exception for *G. fascicularis* and *P. contigua* (Table 5). On the other hand, at 33 psu, partial mortality was relatively lower than at 20 psu, with higher partial mortality only observed in *P. damicornis* and *S. pistillata*'s fragments (Table 5), which indicates that the decrease in salinity of 13 psu was detrimental for all the coral species in study.

Significant intraspecific differences were found among treatments: *G. fascicularis* and *P. contigua* at 20 psu (PERMANOVA pair-wise $p < 0.05$, Table 5). In the low salinity treatment they reached the class [75,100] in low percentages (30% and 15%, respectively), whilst in the high temperature + low salinity treatment they reached it in high

Table 3
Summary of results of PERMANOVA permutation tests applied to report the effects of coral species, temperature, salinity, and injury in coral fragments' partial mortality, growth, and regeneration rates. Significant differences are marked a bold.

	df	SS	MS	Pseudo-F	p (perm)
Partial mortality					
Coral species	8	2.5×10^5	3.1×10^4	68.5	**0.000**
Temperature	9	2.4×10^5	2.6×10^4	57.2	**0.000**
Salinity	9	3.9×10^6	4.3×10^5	945.1	**0.000**
Injury	9	3.8×10^3	4.3×10^2	0.9	0.525
Temperature × Salinity	9	2.5×10^5	2.7×10^4	60.1	**0.000**
Temperature × Injury	9	3.3×10^3	3.6×10^2	0.8	0.689
Salinity × Injury	9	4.9×10^3	5.4×10^2	1.2	0.262
Temperature × Salinity × Injury	9	3.3×10^3	3.7×10^2	0.8	0.684
Growth rate					
Coral species	8	14.5	1.8	99.4	**0.000**
Temperature	7	14.5	2.1	113.3	**0.000**
Salinity	2	4.6	2.3	126.1	**0.000**
Injury	9	0.2	2.5 × 10–2	1.4	0.194
Temperature × Salinity	1	2.2×10^{-3}	2.2×10^{-3}	0.1	0.713
Temperature × Injury	7	0.2	3.5 × 10–2	1.9	0.074
Salinity × Injury	2	6.6 × 10–3	3.3 × 10–3	0.2	0.822
Temperature × Salinity × Injury	1	6.1 × 10–3	6.1 × 10–3	0.3	0.552
Regeneration rate					
Coral species	8	3.7	0.5	13.0	**0.000**
Temperature	9	2.2	0.2	6.9	**0.000**
Salinity	2	0.7	0.3	9.6	**0.000**
Temperature × Salinity	2	0.4	0.2	5.6	**0.010**

Table 4
Mortality rate of the nine coral species studied on specific days of the four experiments. C – Control, HT – High temperature, LS – Low salinity.

	Ce										HT										LS										HT + LS									
Species\days	2	3	4	5	6	10	20	40	60		2	3	4	5	6	10	20	40	60		2	3	4	5	6	10	20	40	60		2	3	4	5	6	10	20	40	60
A. tenuis	0	0	10	10	10	10	10	10	10		0	0	0	0	0	0	0	0	0		20	50	65	100	100	100	100	100	100		100	100	100	100	100	100	100	100	100
M. capricornis (BM)	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	0	0	10	40	65	90	90	100		50	70	95	95	100	100	100	100	100
M. capricornis (GM)	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	5	10	10	15	30	75	100	100		65	100	100	100	100	100	100	100	100
T. reniformis	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	0	0	0	100	100	100	100	100		0	25	65	100	100	100	100	100	100
E. lamellosa	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	25	60	90	100	100	100	100	100		90	100	100	100	100	100	100	100	100
G. fascicularis	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	0	0	0	10	15	30	30	30		0	15	40	55	55	65	70	75	75
P. damicornis	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	5	85	100		0	0	5	85	100	100	100	100	100		0	70	100	100	100	100	100	100	100
S. pistillata	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	5	100		0	30	50	80	85	95	95	95	100		0	25	55	90	100	100	100	100	100
P. contigua	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0	5	5		0	0	0	0	0	0	85	100	100

percentages (75% and 100%, respectively; Table 5).

3.1.3. Coral condition

In the control treatment, only *A. tenuis* presented mortality (10%, Table 6). All the other coral species displayed their normal coloration throughout the course of the experiment (Table 6).

In the high temperature treatment, the fragments of *A. tenuis*, *M. capricornis* (GM), *E. lamellosa,* and *G. fascicularis* remained normal throughout the 60 days experiment (Table 6). 75% of the fragments of *M. capricornis* (BM) and *P. contigua* were pale on the 60th day of experiment, while *T. reniformis* fragments were completely paled on the 40th day (Table 6). Since the 20th day of experiment, a decrease in the percentage of bleached fragments was evident in *P. damicornis* and *S. pistillata* fragments (80% and 5%, respectively) due to them succumbing to mortality that reached 100% on the last day of the experiment (Table 6). These results indicate that *M. capricornis* (BM), *T. reniformis,* and *P. contigua* probably experienced some degree of heat stress in this treatment, displayed as color attenuation though never reaching the bleached condition, whereas *P. damicornis* and *S. pistillata* appear to be highly susceptible to heat stress, due to their complete mortality in this treatment.

In the low salinity treatment, *A. tenuis*, *T. reniformis*, *E. lamellosa,* and *P. damicornis* fragments perished in the first 20 days of experiment (Table 6). A decrease in the percentage of bleached fragments was evident in *M. capricornis* (BM), *M. capricornis* (GM), and *S. pistillata*. *M. capricornis* (GM) fragments started it by the 20th day with a decrease of 15%, while *M. capricornis* (BM) and *S. pistillata* started it latter, on the 40th day, with a decrease of 10% and 5%, respectively, due to them succumbing to mortality that reached the 100% on the 40th day for *M. capricornis* (GM) and on the 60th day for *M. capricornis* (BM) and *S. pistillata.* (Table 6). On the other hand, a decrease in the percentage of pale fragments was evident in *G. fascicularis* and *P. contigua* fragments, by the 20th day for *G. fascicularis* and the 40th day for *P. contigua* (5% and 45%, respectively), due to them becoming bleached. These two coral species were the only ones that did not reach 100% mortality (Table 6). These results indicate that *G. fascicularis* and *P. contigua* were the coral species most tolerant to this treatment, since these coral species only reached the dead condition in low percentages (30% and 5%, respectively).

In the high temperature + low salinity treatment, the fragments of *A. tenuis, M. capricornis* (both morphotypes), *T. reniformis, E. lamellosa, P. damicornis,* and *S. pistillata* presented 100% mortality in the first 20 days of experiment (Table 6), whilst *P. contigua* only perished on the 40th day (Table 6). *G. fascicularis* reached the bleached condition on the 20th day of experiment and the percentage of dead fragments reached 75% (Table 6). These results indicate that *G. fascicularis* was the only coral species tolerant to the full extent of this treatment, displayed by its survival rate of 25% on the 60th of experiment.

3.2. Growth rate

Growth rate was significantly affected by the independent effects of coral species, temperature, and salinity (PERMANOVA $p < 0.05$, Table 3). Most coral species showed significant intraspecific differences between control and high temperature treatments (PERMANOVA pair-wise $p < 0.05$, Table 7), being highest in the control treatment, except for *G. fascicularis* that presented similar growth rates between these two treatments (PERMANOVA pair-wise $p > 0.05$, Table 7). *G. fascicularis* and *P. contigua* fragments showed significant intraspecific differences in growth rate between control and low salinity treatments, being highest in the control treatment (PERMANOVA pair-wise $p < 0.05$, Table 7). *G. fascicularis* fragments also presented significant intraspecific growth rate differences between high temperature and high temperature + low salinity treatments, being highest in the high temperature treatment (PERMANOVA pair-wise $p < 0.05$, Table 7). These results indicate that high temperature, low salinity, and high temperature + low salinity

Table 5
Partial mortality rate of the nine coral species studied every 20 days of the four experiments (C – control, HT – High temperature, LS – low salinity) and separated in percentage classes [0,25%], [25,50%], [50,75%], and [75,100%].

		C				HT				LS				HT + LS			
Time	Species	[0,25]	[25,50]	[50,75]	[75,100]	[0,25]	[25,50]	[50,75]	[75,100]	[0,25]	[25,50]	[50,75]	[75,100]	[0,25]	[25,50]	[50,75]	[75,100]
20	*A. tenuis*	90	0	0	10	100	0	0	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	100	0	0	0	10	0	0	90	0	0	0	100
	M. capricornis (GM)	100	0	0	0	85	15	0	0	5	5	5	85	0	0	0	100
	T. reniformis	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	95	0	5	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	20	30	20	30	0	0	30	70
	P. damicornis	100	0	0	0	95	0	0	5	0	0	0	100	0	0	0	100
	S. pistillata	100	0	0	0	100	0	0	0	5	0	0	95	0	0	0	100
	P. contigua	95	5	0	0	100	0	0	0	90	5	5	0	5	0	0	95
40	*A. tenuis*	90	0	0	10	85	10	5	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	100	0	0	0	0	0	10	90	0	0	0	100
	M. capricornis (GM)	100	0	0	0	30	55	15	0	0	0	0	100	0	0	0	100
	T. reniformis	100	0	0	0	95	5	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	90	5	5	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	0	0	70	30	0	0	25	75
	P. damicornis	100	0	0	0	15	0	0	85	0	0	0	100	0	0	0	100
	S. pistillata	100	0	0	0	50	25	5	20	0	0	5	95	0	0	0	100
	P. contigua	95	5	0	0	100	0	0	0	45	25	15	15	0	0	0	100
60	*A. tenuis*	90	0	0	10	75	25	0	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	M. capricornis (GM)	90	5	5	0	65	35	0	0	0	0	0	100	0	0	0	100
	T. reniformis	100	0	0	0	95	5	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	85	10	5	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	0	0	70	30	0	0	25	75
	P. damicornis	100	0	0	0	0	0	0	100	0	0	0	100	0	0	0	100
	S. pistillata	95	5	0	0	0	0	0	100	0	0	0	100	0	0	0	100
	P. contigua	90	0	10	0	100	0	0	0	45	25	15	15	0	0	0	100

Table 6
Coral condition of the nine coral species studied every 20 days of the four experiments (C – Control, HT – High temperature, LS – Low salinity) and separated in four categories: normal, pale, bleached, and dead.

		C				HT				LS				HT + LS			
Time	Species	normal	pale	bleached	dead	normal	pale	bleached	dead	normal	pale	bleached	dead	normal	pale	bleached	dead
20	*A. tenuis*	90	0	0	10	100	0	0	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	100	0	0	0	0	0	10	90	0	0	0	100
	M. capricornis (GM)	100	0	0	0	100	0	0	0	0	10	15	75	0	0	0	100
	T. reniformis	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	0	5	65	30	0	0	30	70
	P. damicornis	100	0	0	0	0	0	95	5	0	0	0	100	0	0	0	100
	S. pistillata	100	0	0	0	0	0	100	0	0	0	5	95	0	0	0	100
	P. contigua	100	0	0	0	100	0	0	0	100	0	0	0	15	0	0	85
40	*A. tenuis*	90	0	0	10	100	0	0	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	100	0	0	0	0	0	10	90	0	0	0	100
	M. capricornis (GM)	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	T. reniformis	100	0	0	0	0	100	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	0	0	70	30	0	0	25	75
	P. damicornis	100	0	0	0	0	0	15	85	0	0	0	100	0	0	0	100
	S. pistillata	100	0	0	0	0	0	95	5	0	0	5	95	0	0	0	100
	P. contigua	100	0	0	0	100	0	0	0	30	60	5	5	0	0	0	100
60	*A. tenuis*	90	0	0	10	100	0	0	0	0	0	0	100	0	0	0	100
	M. capricornis (BM)	100	0	0	0	25	75	0	0	0	0	0	100	0	0	0	100
	M. capricornis (GM)	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	T. reniformis	100	0	0	0	0	100	0	0	0	0	0	100	0	0	0	100
	E. lamellosa	100	0	0	0	100	0	0	0	0	0	0	100	0	0	0	100
	G. fascicularis	100	0	0	0	100	0	0	0	0	0	70	30	0	0	25	75
	P. damicornis	100	0	0	0	0	0	0	100	0	0	0	100	0	0	0	100
	S. pistillata	100	0	0	0	0	0	0	100	0	0	0	100	0	0	0	100
	P. contigua	100	0	0	0	25	75	0	0	20	15	60	5	0	0	0	100

Table 7
Coral species' average growth rate ± standard deviation (% day^{-1}) in the four experiments. C – Control, HT – High temperature, LS – Low salinity. NA – Not Available.

Species	C	HT	LS	HT + LS
A. tenuis	1.13 ± 0.21	0.49 ± 0.10	NA	NA
M. capricornis (BM)	0.73 ± 0.13	0.30 ± 0.18	NA	NA
M. capricornis (GM)	0.64 ± 0.15	0.13 ± 0.05	NA	NA
T. reniformis	0.44 ± 0.16	0.22 ± 0.08	NA	NA
E. lamellosa	0.43 ± 0.27	0.16 ± 0.05	NA	NA
G. fascicularis	0.26 ± 0.07	0.26 ± 0.09	0.07 ± 0.03	0.03 ± 0.03
P. damicornis	0.92 ± 0.14	NA	NA	NA
S. pistillata	0.62 ± 0.14	NA	NA	NA
P. contigua	1.08 ± 0.17	0.36 ± 0.10	0.40 ± 0.12	NA

treatments affected negatively coral species' growth when compared with control treatment, displayed as growth rate decrease in these three treatments.

In the control treatment, the highest growth rates were observed in *A. tenuis* and *P. contigua* fragments (PERMANOVA pair wise $p < 0.05$) (1.13 ± 0.21% day^{-1} and 1.08 ± 0.17% day^{-1}, respectively; PERMANOVA pair wise $p > 0.05$), whereas the lowest one was observed in *G. fascicularis* fragments (0.26 ± 0.07% day^{-1}, PERMANOVA pair wise $p < 0.05$; Table 7). In the high temperature treatment, the highest growth rate was observed in *A. tenuis* fragments (0.49 ± 0.10% day^{-1}, PERMANOVA pair wise $p < 0.05$), whereas the lowest ones were observed in *E. lamellosa* and *M. capricornis* (GM) fragments (PERMANOVA pair wise $p < 0.05$) (0.16 ± 0.05% day^{-1} and 0.13 ± 0.05% day^{-1}, respectively; PERMANOVA pair wise $p > 0.05$; Table 7). In the low salinity treatment, the highest growth rate was observed in *P. contigua* fragments (0.40 ± 0.12% day^{-1}, PERMANOVA pair wise $p < 0.05$), while the lowest one was observed in *G. fascicularis* fragments (0.07 ± 0.03% day^{-1}, PERMANOVA pair wise $p < 0.05$; Table 7). These results indicate that branching corals have higher growth rates than plate, encrusting, and massive coral species.

3.3. Regeneration rate

Regeneration rate was significantly affected by the independent effects of coral species, temperature, and salinity (PERMANOVA $p < 0.05$, Table 3). There was also a significant effect of the interactions of temperature and salinity (PERMANOVA $p < 0.05$, Table 3). Almost all coral species presented significant intraspecific differences between control and high temperature treatments, with higher regeneration rates in the high temperature treatment (PERMANOVA pair-wise $p < 0.05$, Table 8), except for *M. capricornis* (GM), *P. damicornis,* and *S. pistillata* that presented similar regeneration rates between these two treatments (PERMANOVA pair-wise $p > 0.05$, Table 8). *G. fascicularis* and *P. contigua* fragments presented similar regeneration rates between low salinity and high temperature + low salinity treatments (PERMANOVA pair-wise $p > 0.05$, Table 8). *P. contigua* fragments presented significant intraspecific differences between high temperature and high temperature + low salinity treatments, with higher regeneration rates in the high temperature treatment (PERMANOVA pair-wise $p < 0.05$, Table 8). On the other hand, both *G. fascicularis* and *P. contigua* fragments presented similar intraspecific regeneration rates between control and low salinity treatments (PERMANOVA pair-wise $p > 0.05$, Table 8). These results indicate that regeneration rates increased with temperature, which is related with an increase in metabolism, being highest in the high temperature treatment and lowest at 20 psu as salinity decreased, probably a result of osmotic stress.

In the control treatment, *S. pistillata* fragments presented the highest regeneration rate (0.65 ± 0.29 mm^2 day^{-1}, PERMANOVA pair wise $p < 0.05$), whereas the lowest ones were presented by *M. capricornis* (BM), *T. reniformis,* and *M. capricornis* (GM) fragments (PERMANOVA pair wise $p < 0.05$) (0.24 ± 0.16 mm^2 day^{-1}, 0.16 ± 0.10 mm^2 day^{-1} and 0.17 ± 0.03 mm^2 day^{-1}, respectively; PERMANOVA pair-wise $p > 0.05$, Table 8). In the high temperature treatment, *G.*

Table 8
Coral species' average regeneration rate ± standard deviation ($mm^2\ day^{-1}$) in the four experiments. C – Control, HT – High temperature, LS – Low salinity. *Only one individual. NA – Not Available.

Species	C	HT	LS	HT + LS
A. tenuis	0.23 ± 0.09	0.42 ± 0.22	NA	NA
M. capricornis (BM)	0.24 ± 0.16	0.69 ± 0.21	NA	NA
M. capricornis (GM)	0.17 ± 0.03	0.16 ± 0.07	NA	NA
T. reniformis	0.16 ± 0.10	0.35 ± 0.16	NA	NA
E. lamellosa	0.30 ± 0.11	0.58 ± 0.27	NA	NA
G. fascicularis	0.30 ± 0.06	0.73 ± 0.27	0.26 ± 0.14	0.16 ± 0.00*
P. damicornis	0.40 ± 0.13	0.50 ± 0.25	NA	NA
S. pistillata	0.65 ± 0.29	0.71 ± 0.32	NA	NA
P. contigua	0.22 ± 0.10	0.59 ± 0.27	0.14 ± 0.05	0.18 ± 0.10

fascicularis, *S. pistillata*, *M. capricornis* (BM), *P. contigua*, *E. lamellosa,* and *P. damicornis* fragments had the highest regeneration rates (PERMANOVA pair wise $p < 0.05$) (0.73 ± 0.27 $mm^2\ day^{-1}$, 0.71 ± 0.32 $mm^2\ day^{-1}$, 0.69 ± 0.21 $mm^2\ day^{-1}$, 0.59 ± 0.27 $mm^2\ day^{-1}$, 0.58 ± 0.27 $mm^2\ day^{-1}$, 0.50 ± 0.25 $mm^2\ day^{-1}$, respectively; PERMANOVA pair-wise $p > 0.05$), whereas *M. capricornis* (GM) fragments showed the lowest regeneration rate (0.16 ± 0.07 $mm^2\ day^{-1}$, PERMANOVA pair wise $p < 0.05$, Table 8). In the low salinity treatment, the highest regeneration rate was observed in *G. fascicularis* (0.26 ± 0.14 $mm^2\ day^{-1}$, PERMANOVA pair wise $p < 0.05$) and the lowest in *P. contigua's* fragments (0.14 ± 0.05 $mm^2\ day^{-1}$, PERMANOVA pair wise $p < 0.05$, Table 8). These results indicate that regeneration rate differences among these coral species do not have a pattern associated with coral morphology.

4. Discussion

This study shows the differential vulnerability of reef-forming coral species towards conditions of warming and low salinity, which will negatively affect the ability of their fragments to regenerate and grow after being separated from their parent colonies, potentially leading to a major shift in tropical coral reef ecosystems' biodiversity.

4.1. Mortality

In the high temperature treatment, the coral species *P. damicornis* and *S. pistillata* had the highest susceptibility to heat stress during the study, displaying the worst coral condition and earlier tissue loss compared to other species. Branching pocilloporids (e.g. *Pocillopora damicornis* and *Stylophora pistillata)* are cited in many reports, both in experimental work (Dias et al., 2018; Jokiel and Coles, 1974) and in the field (Glynn, 1983; Loya et al., 2001), as being taxa severely damaged by heat stress, mainly due to their morphology (Brown and Howard, 1985; Hoegh-Guldberg and Salvat, 1995), since branching corals die more often than encrusting and massive growth forms (Marshall and Baird, 2000; McClanahan et al., 2002). However, other factors affecting coral species susceptibility to heat stress must also be considered, such as *Symbiodinium* clade (Magalon et al., 2007), tissue thickness (Loya et al., 2001), respiratory rates (Jokiel and Coles, 1990), mucus production rate (Fitt et al., 2009), tissue concentration of fluorescent pigments (FPs; Salih et al., 1998), and heterotrophic feeding capacity (Grottoli et al., 2006). According to the characteristics of the coral species described in Table 1, both *P. damicornis* and *S. pistillata* can harbor *Symbiodinium* clade C, which is consistent with their high susceptibility to heat stress (Rowan et al., 1997). Nevertheless, all the coral species in study can harbor *Symbiodinium* clade C so, in this case, we cannot say that *Symbiodinium* clade was a factor influencing their higher susceptibility to heat stress. Regarding all the other factors aforementioned, pocilloporids are known as having thinner tissues (Hoegh-Guldberg and Salvat, 1995), the greatest respiratory rates (Frakzisket, 1970), very low mucus production (Frakzisket, 1970; Fitt et al., 2009), relatively low densities of FPs (Salih et al., 1998), and a very limited heterotrophic capacity (Houlbrèque and Ferrier-Pagès, 2009; Ziegler et al., 2014) when compared with other taxa. Those inherent traits are consistent with *P. damicornis* and *S. pistillata* higher susceptibility to heat stress (Fitt et al., 2009; Grottoli et al., 2006; Hoegh-Guldberg, 1999; Jokiel and Coles, 1990; Salih et al., 1998). Another aspect to have into account is the life-history strategies of the coral species in study, *P. damicornis* and *S. pistillata* are considered "weedy" corals (Darling et al., 2012), defined as small corals with brooding reproduction, fast growth rates and high population turnover (Knowlton, 2001), and weedy corals have been considered sensitive to heat stress in the Indo-Pacific (Darling et al., 2013).

Mortality and partial mortality were higher at 20 psu than at 33 psu, such reductions in salinity are known to be potentially lethal to corals, in part due to corals' limited osmoregulation capacity (Ferrier-Pagès et al., 1999; Kerswell and Jones, 2003; Manzello and Lirman, 2003). Observations in previous studies, both in experimental work (Edmondson, 1928) and in the field (Coles and Jokiel, 1992; Jokiel et al., 1993), have supported the estimates of 15 psu to 20 psu for 24 h or more as the lower lethal salinity in scleractinian corals. Many reports refer to salinity reductions causing massive coral and reef organism mortality and it is during major storm events that its effects on coral reefs are most devastating (Blakeway, 2004; Goreau, 1964; van Woesik et al., 1995).

The mortality results obtained in the low salinity treatment indicate that the tolerance to hyposaline stress is highly species-specific. The pocilloporids *Pocillopora damicornis* and *Stylophora pistillata* and the genus *Acropora* were already known to be highly sensitive to lowered salinity (Blakeway, 2004; Ferrier-Pagès et al., 1999; Jokiel et al., 1993; Kerswell and Jones, 2003; Moberg et al., 1997). However, as all the fragments of *T. reniformis* and *E. lamellosa* perished on the 6th day of experiment, and most of the fragments of *M. capricornis* (both morphotypes) perished on the 20th day, we show that these species are also highly sensitive to lowered salinity, which was previously unknown. Most of *G. fascicularis* and *P. contigua* fragments survived for 60 days in the low salinity treatment, confirming these species exceptional tolerance to low salinity (van Woesik, 1994; Xiubao et al., 2009).

High mortality in the high temperature-low salinity treatment indicates that long-term synergy of higher temperature and lower salinity is very detrimental to all coral species tested, leading to the death of most of the coral fragments on the 6th day of the experiment. This synergistic effect had already been documented in other studies (Coles and Jokiel, 1978; Mayfield and Gates, 2007; Xiubao et al., 2009). Only *P. contigua* showed higher tolerance, with its fragments lasting for 40 days under these conditions. *G. fascicularis* proved to be the most resistant species to the synergy of higher temperature and lower salinity, surviving the whole 60-day experiment, albeit only with 25% of the fragments still alive by the end of the experiment. The results obtained in this treatment indicate that even short-term exposure of two days to salinities of 20 psu reduces the tolerance of several coral species to high temperature.

4.2. Coral condition

Understanding the variation in coral species response to heat and hyposaline stressors is necessary to accurately predict how coral reefs condition and population structure will change in a climate change scenario of high temperature and low salinity. In the control treatment almost all the coral species remained unbleached throughout the course of the experiment. In the high temperature treatment, *P. damicornis* and *S. pistillata* fragments were the only ones that reached the bleached condition and 100% mortality, which reveal that these two species are highly susceptible to heat stress.

In the low salinity treatment, four out of the nine coral species presented 100% mortality in the first 20 days of experiment without previous fragments' discoloration, *A. tenuis*, *T. reniformis*, *E. lamellosa,* and *P. damicornis*. On the other hand, the coral species *M. capricornis* (BM), *M. capricornis* (GM), *S. pistillata*, *G. fascicularis*, and *P. contigua* showed tissue discoloration, before complete mortality in the first three coral species. The discoloration of corals following osmotic stress is caused by the breakdown in coral-zooxanthellae symbiosis and it has been observed in other studies (Goreau, 1964; Kerswell and Jones, 2003), however, when a coral species cannot cope with the osmotic stress it perishes without previous discoloration (Hoegh-Guldberg and Smith, 1989; Jokiel et al., 1993). Coral death was followed by immediate tissue sloughing off which revealed the underlying white calcareous skeleton, although *T. reniformis* fragments became covered by thick whitish-brown slime and its coenosarc disintegrated into mucous blebs.

In the high temperature + low salinity treatment, seven out of the nine coral species showed complete mortality in the first 20 days of experiment without previous fragments' discoloration, *A. tenuis*, *M. capricornis* (both morphotypes), *T. reniformis*, *E. lamellosa*, *P. damicornis* and *S. pistillata*. The synergistic effects of high temperature and low salinity were more than these coral species could cope with. Nevertheless, *G. fascicularis* although presenting some percentage of bleached fragments, did not present 100% mortality.

4.3. Growth

Coral growth is affected by environmental parameters such as sea surface temperature and salinity (Lough and Cooper, 2011), and measuring coral growth has become relevant as an indicator of possible degradation of coral reefs due to climate change (Anthony et al., 2011; Buddemeier et al., 2004; Manzello, 2010; Manzello et al., 2008). Coral fragments' growth rates decreased with increase in water temperature, this is in agreement with physiological data presenting an accentuated decline in coral growth at temperatures only a few degrees above optimum levels (Berkelmans and Willis, 1999). Growth rates also decreased as salinity decreased, which is corroborated by other studies stating that scleractinian corals exposed to rapid environmental fluctuations may exhibit a limited capacity for osmoregulation (Mayfield and Gates, 2007; Ranklin and Davenport, 1981), and that the prolonged exposure to salinity stress can affect coral growth (Coles and Jokiel, 1992; Porter et al., 1999).

Our results are also in accordance with another study showing that corals' growth rates decrease if salinity changes by ± 2 psu from optimal values (Ferrier-Pagès et al., 1999). In all treatments, *A. tenuis* and *P. contigua* presented the highest growth rates, with the exception of *A. tenuis* at 20 psu and *P. contigua* in the high temperature + low salinity treatment where they died. According with Guest et al. (2011), plate and massive morphologies grow slower than branched ones. Having this in mind, the lower growth rates of *M. capricornis* (GM) and *E. lamellosa* in the high temperature treatment, and the ones of *G. fascicularis* at 26 °C for both salinities can thus be explained. *G. fascicularis* fragments were the only ones that showed similar growth rate at 26 °C and 30 °C for both salinities, suggesting that this coral species is resistant to this level of heat stress. All the other coral species presented their highest growth rates in the control treatment, probably as a result of heat stress in the high temperature treatment (Fine et al., 2002; Szmant and Gassman, 1990).

4.4. Regeneration

Understanding how extrinsic factors such as seawater temperature and salinity limit regeneration in corals is crucial since poor regenerative ability can lead to a reduction in colony fitness (Hall, 1997). The regeneration rate of the coral species studied generally increased with temperature increment. This is expected since increase in water temperatures accelerates coral fragments' metabolism and, as long as their specific stress levels are not achieved, their regeneration rates will be greater at higher temperatures. In addition, regeneration rate decreased in hyposaline conditions, which is also expected since low salinity is known to affect regeneration due to its negative effects on coral metabolism (Jokiel et al., 1993; Moberg et al., 1997). Coral species regenerative ability could not be ranked as in Hall (1997) probably because the experimental conditions, methodology, and coral species were different. In the low salinity treatment, regeneration rate of the only two species that survived (*P. contigua* and *G. fascicularis*) was not negatively impacted compared with the control treatment, whereas in the high temperature treatment most of the coral species presented increase in regeneration rates, exception of the coral species negatively impacted by heat stress. According to Hall (1997), branching corals present the highest regenerative ability, which in this study correspond to the ones most affected by heat and hyposaline stress. Thus, the use of different stress treatments may have altered the regenerative ability of the coral species in study.

The high mortality rates registered in the high temperature + low salinity treatment deter conclusions regarding regeneration. In the only species that survived the 60 days in this treatment, *G. fascicularis*, regeneration capacity was negatively impacted compared to control treatment.

Differential susceptibility and mortality among species can exert a major influence on coral community structure (Pratchett, 2001). According with the results obtained in this study, it is expected that the coral species *G. fascicularis* will be more resistant in a warmer ocean, especially in coastal areas prone to low salinity episodes, and thus becoming more important in terms of coral cover. Nevertheless, it is important to have in consideration that this is a slow-growing coral species and may take a long time until increase in coral cover can be observed. On the other hand, other disturbances present in their natural habitat need to be taken into account, such as competition (Baird and Hughes, 2000), predation (Pratchett, 2001), and extreme events (tropical storms, Fabricius et al., 2008) that, like heat and hyposaline stress, affect with greater magnitude fast-growing coral species (Dias et al., 2018; True, 2012). Thus, the predicted increase in temperature and both frequency and intensity of tropical storms will likely cause local eradication or prevent susceptible species from resettle and will allow *G. fascicularis*' dominance.

This study focused on the interaction of high temperature and low salinity associated with the increase in frequency and intensity of tropical storms in the Indo-Pacific oceans, however, it needs to be cautioned that other environmental variables not tested in this study can be altered by global climate change (e.g. ultraviolet radiation levels (Hoegh-Guldberg and Bruno, 2010) and pH (Manzello, 2010)) and that alterations in the environmental variables studied may also happen, such as an increase in mean daily maximum temperature (Wergen and Krug, 2010), mean salinity (Durack et al., 2013), and sea surface temperatures (SST; Collins et al., 2010). Actually, other possible combinations of the environmental variables studied can be possible in the Indo-Pacific region, such as elevated temperatures and elevated salinity, due to lack of rainfall in the Pacific region, often for months determined by the IPO and ENSO phases (Dong and Dai, 2015), or due to increased evaporation in already dry regions, such as temperate

Australia, making those regions saltier (Durack et al., 2012). Thus, our study only shows one of many possible scenarios.

5. Conclusions

Resistance capacity of most corals was overcome in long-term treatments at 20 psu. The coral species *G. fascicularis* and *P. contigua* were the most resistant to salinity stress. *G. fascicularis* fragments were the only ones that withstood the synergistic effects of high temperature and low salinity. This knowledge may have ecological implications in the understanding of coral reef biodiversity changes in the near future, as well as in coral reef conservation and management.

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